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Conus pennaceus from Madagascar – a complex of geographical subspecies (Gastropoda: Conidae)

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With 6 plates, 14 figures and 2 tables

Summary

Two previously unnamed subspecies of *Conus pennaceus* Born, 1778 (Gastropoda: Conidae) from S Madagascar are described and compared to further geographical subspecies and populations of *Conus pennaceus* from the S Madagascan area as well as from the E African coast. The marine surface currents around Madagascar are supposed to play an important role in producing genetic isolation between the *Conus pennaceus* populations. S.E.M. photographs of radular teeth of *Conus pennaceus vezoi* n.ssp. and *Conus textile* Linné, 1758 ("form *sirventi*") from Madagascar are presented and the results are discussed.

Zusammenfassung

Zwei neue Unterarten von *Conus pennaceus* Born, 1778 (Gastropoda: Conidae) aus Südmadagaskar werden beschrieben und mit weiteren geographischen Unterarten und Populationen aus Südmadagaskar sowie aus Ostafrika verglichen. Die marinen Strömungsverhältnisse um Madagaskar werden als bedeutende Isolationsmechanismen diskutiert. Radulapräparate von *Conus pennaceus vezoi* n.ssp. und *Conus textile* Linné, 1758 („Form *sirventi*"), beide von Madagaskar, werden mittels R.E.M.-Aufnahmen abgebildet und diskutiert.

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1. Introduction

Conus pennaceus Born, 1778 as assessed by RÖCKEL, KORN & KOHN (1995) represents a polytypic species, or possibly a superspecies (species group sensu MAYR). The lectotype of *C. pennaceus* (designated by KOHN 1964) is strikingly matched by shells from northern Mozambique. The lectotype of *C. praelatus* Hwass in Bruguière, 1792 (designated by KOHN 1968) is a shape variant of typical *C. pennaceus.* At least the Hawaiian population of *C. pennaceus* has to be considered a geographical subspecies (RÖCKEL et alii, 1995), although still unnamed. Therefore *C. pennaceus* from northern Mozambique is here regarded as the nominal subspecies *C. p. pennaceus* (the taxonomical status of "form *elisae*" from northern Mozambique needs further research: variant of *C. p. pennaceus* or geographical subspecies).

Populations of *C. pennaceus* from southern Mozambique to southern Natal (Ilha do Bazaruto, Massinga area, Ponta da Barra to S Natal) intergrade conchologically (RÖCKEL et alii, 1995: 299). This justifies to reject the ranking of *C. lohri* Kilburn, 1972 as a separate species. However, why should we deny the subspecies status for the complex of these 3 populations? As their shells differ from those of *C. p. pennaceus* a subspecific ranking must be taken into consideration.

Is *C. rubiginosus* Hwass in Bruguière, 1792, as represented by the lectotype (designated by KOHN 1968), really identical with those shells from Mauritius and St. Brandon which are sold under this name? Are those Mascarene shells a geographical or a bathymetrical subspecies or perhaps a valid species? Did we really verify the status of *C. echo* Lauer, 1988 and *C. madagascariensis* Sowerby II, 1858 as valid species?

To shed light on the complex taxonomic relations between the so-called *C. pennaceus* populations examination of the animals is necessary (incl. DNA analysis and examination of the radular teeth). However, at present it seems impossible to obtain such data. A first step might be to achieve a reliable correlation between conchological morphs and localities. Knowing the locality and the habitat of the morphs, we will be able to separate geographic isolates (MAYR & ASHLOCK, 1991: 50) from ecomorphs or individual variants.

Thanks to the knowledge of one of the authors (M. BLÖCHER) on the occurrence of *C. pennaceus* in Madagascar, we can give a first résumé of morphs and localities of this *Conus* from southeastern to southwestern Madagascar (from Taolañaro westward to Morombe).

However, we must admit that we need more information to verify reports of *C. pennaceus* from localities outside the mentioned range. We also admit that our ecological data are poor. Nevertheless, one can see *C. pennaceus* lined up between Taolañaro and Morombe in several geographically separated local populations that may differ conchologically as much to a degree that justifies a separation as geographical subspecies.

The linear distances between the single populations may differ considerably: There are 25 km air-line between the populations from Maromitiliky and Pointe Be-

heloka, and 120 km between those from Beheloka and Manombo without any *C. pennaceus* locality in between (Fig. 2).

2. Acknowledgments, materials and methods

2.1. Acknowledgments

For the E.S.E.M.-photographs of the radular teeth of *C. pennaceus vezoi* n.ssp. we are indebted to Edeltraud Materna-Morris (Karlsruhe). For the S.E.M.-photographs of the radular teeth of *C. pennaceus vezoi* n.ssp and *C. textile* Linné, 1758 ("form *sirventi*") we thank Susanne Leidenroth (Stuttgart). The colour photographs were taken by Annette Schultheiss (Stuttgart). We would specially like to thank Fernand Corbier (Rodez, France), who donated the alcohol preserved material of *C. pennaceus vezoi* n.ssp., and Dr. Ronald Fricke (Stuttgart) for the critical revision of the manuscript.

2.2. Materials

Specimens in the following collections were examined:

CB – Private Collection Manfred Blöcher, Duisburg, Germany;
CK – Private Collection Werner Korn, Neustadt, Germany;
NMC – Collection of the *N*aturkunde-*M*useum *C*oburg, Germany;
SMNS– Collection Da Motta and collection Röckel in the collection of the *S*taatliches *M*useum für *N*aturkunde *S*tuttgart, Germany.

All types signed herein CK were donated to SMNS, except otherwise stated.

Further abbreviations used for shell morphometry refer to those used by Röckel et alii (1995):

L – Shell *L*ength in mm;
RW – *R*elative *W*eight = absolute weight/L; grams/mm;
RD – *R*elative *D*iameter = maximum diameter/aperture height;
PMD – *P*osition of *M*aximum *D*iameter = height of maximum diameter/aperture height;
RSH – *R*elative *S*pire *H*eight = (shell length – aperture height)/shell length.

For examination, 19 empty shells of *C. pennaceus tsara* without periostracum had been available (11 adults, 8 subadults). As for *C. pennaceus vezoi,* we examined 4 shells with periostracum and containing parts of the animals (only 1 specimen furnished radular teeth) as well as 23 shells without animal or periostracum. From one specimen of *C. textile* Linné, 1758 ("*sirventi* form") from Madagascar we could examine radular teeth for comparison. All parts of the animals were fixed in ethanol (70%).

2.3. Methods

Preparation of the radular teeth for S.E.M. or E.S.E.M. (Evaporation Scanning Electron Microscope = S.E.M. under humid atmosphere): Mazeration of the animal in KOH or NaOH and dissection under a binocular microscope. Mature teeth were cleaned in ethanol (99%) and air dried. Individual teeth were mounted on aluminium S.E.M. stubs (diameter 12 mm) with mounting-foil of polycarbonate and graphite. For the scanning electron microscopy in the Forschungszentrum Karlsruhe, Institut für Materialforschung 1, no spattering was necessary. The photographs were taken using a XL 30 E.S.E.M from Philipps. Teeth were coated with a layer of gold-palladium in a vacuum evaporator (Type Edwards S150 B spatter coater) only in the Museum in Stuttgart. The photographs were taken using a ISI-SS40 and exposed on Ilford FP4 125 films.

Abbreviations used for radula morphometry refer to those used by Kohn et alii (1999) and Nishi & Kohn (1999):

T_L/S_L – Relative tooth length = ratio of *T*ooth *L*ength to *S*hell *L*ength;
$B1_L/T_L$ – Relative first barb length = ratio of distance from the apex to first barb ($B1_L$), to *T*ooth *L*ength;
$B2_L/T_L$ – Relative second barb length = ratio of distance from the apex to second barb ($B2_L$), to *T*ooth *L*ength;

3. Effects of marine surface currents in the Southwestern Indian Ocean (Fig. 1)

The information on general surface currents in the following text is mainly based on DIETRICH & ULRICH (1968) and WHIPPLE (1984). In the Mozambique Channel, the major drift is the warm Agulhas Current flowing southward in austral summer and winter along the coasts of Mozambique and South Africa. At the coast of Tanzania the current flows northward during the whole year. Only at the coasts of Kenya and Somalia there is a drift to the south in austral summer and to the north in austral winter. The surface currents along the western coast of Madagascar are almost exclusively triggered by the warm South Equatorial Current; they are constantly directed northward during the entire year. In comparison to the Agulhas Current, the drifts along the Madagascan coast have a low velocity and constancy, though distinct currents may be caused by strong winds during the austral winter.

As a result of the constant one way drift the *C. pennaceus* population of Taolañaro, SE Madagascar is genetically separated from the populations in SW Madagascar. Having a benthic or nearly benthic development in *C. pennaceus* (RÖCKEL et alii, 1995), we could expect a "one-way" gene flow: Genes may go from the southeast to the south-west but no genes will flow back to the south-east.

Along the south-western coast of Madagascar the connection by surface currents is rather limited compared to the situation at the coast of Mozambique and the Republic of South Africa. The currents are constantly directed from the south to the north producing a reproductive isolation – to some extent – in the southern parts of the area Itampolo and Morombe (Fig. 2). Therefore uniformity should evolve in the south rather than in the more northern regions which are influenced by larvae from the southern populations. In the course of time there should arise a genetic divergence between southern and northern populations of the south-west.

The only connection by surface currents between the Mozambique coast and western Madagascar occurs during the southern summer from the area of Nacala (N Mozambique), towards the area of Mahajanga (NW Madagascar). This does not have any effect on the gene pools of the southwestern *C. pennaceus* populations. We have records of *C. pennaceus* coming from this northwestern region of Madagascar. However, these records still need verification.

4. *Conus pennaceus* subspecies from Madagascar

4.1. *Conus pennaceus tsara* n.ssp. (Plate 1)

Holotype: SMNS ZI 30424 (L: 52.7 mm, MD: 26.9 mm).

Paratype 1: CK nº 2557 (L: 55.1 mm, MD: 28.1 mm). – Paratype 2: SMNS ZI 30425 (L: 49.6 mm, MD: 24.4 mm). – Paratype 3: CK nº 2532 (L: 45.3 mm, MD: 25.6 mm). – Paratype 4: SMNS ZI 30426 (L: 44 mm, MD: 23 mm). – Paratype 5: SMNS ZI 30427 (L: 45.4 mm, MD: 21.2 mm). – Paratype 6: ex coll. CK nº 2532 ded. to NMC (L: 43.7 mm, MD: 25 mm). – Paratype 7: CK nº 2531 (L: 32.5 mm, MD: 15.1 mm). – Paratype 8: CK nº 2531 (L: 30.7 mm, MD: 16.1 mm). – Paratype 9: SMNS ZI 30428 (L: 49.3 mm, MD: 23.8 mm). – Paratypes 10–18: SMNS ZI 30429–30437 (L: 51.0–34.4 mm, MD: 25.8–18.4 mm).

Type Locality: Holotype and paratypes from SE Madagascar, Taolañaro (Fort Dauphin) (Fig. 2).

Etymology: "tsara" is a native word and means "nice" or "pretty", which seems justified by the harmony of the colour pattern of this subspecies.

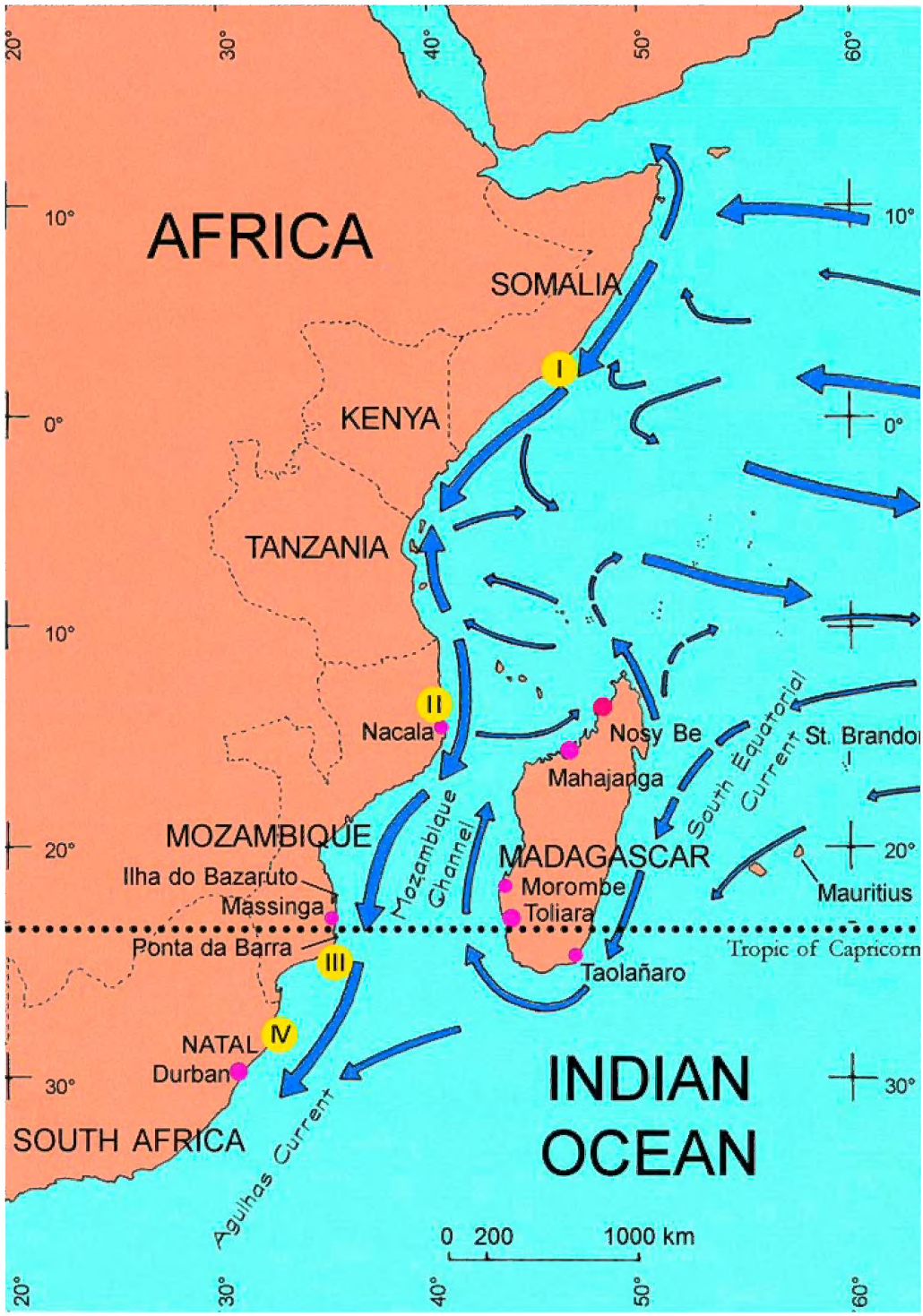


Fig. 1. Surface currents of the Indian Ocean in austral summer near the eastern coast of Africa, especially around South Madagascar and in the Mozambique Channel. – *I) Conus echo*, Somalia; – *II) Conus pennaceus pennaceus & Conus pennaceus* ("form *elisae*"), N Mozambique; – *III–IV) Conus pennaceus* local populations, S Mozambique to Natal (incl. *C. lohri*).

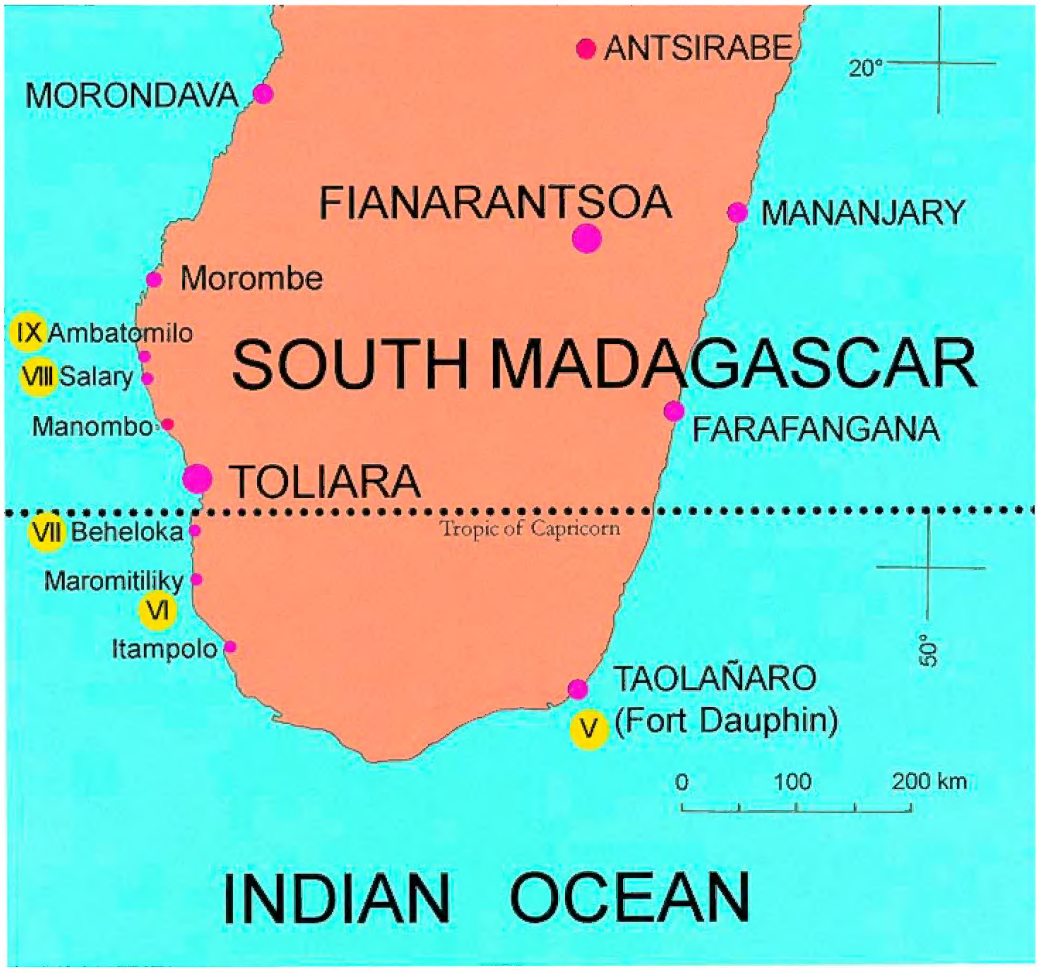


Fig. 2. South Madagascar. – *V) Conus pennaceus tsara* n.ssp., Taolañaro (Fort Dauphin); – *VI) Conus pennaceus vezoi* n.ssp., Maromitiliky; – *VII) Conus pennaceus beheloka-ensis,* Beheloka; – *VIII) Conus pennaceus corbieri,* Salary; – *IX) Conus pennaceus* local population, Ambatomilo.

Tafel 1–6: Filme

Plate 1

Plate 2

Plate 3

Plate 4

Plate 5

Plate 6

Plate 1

Figs. 1–9. *Conus pennaceus tsara* n.ssp. from Taolañaro (Fort Dauphin), Madagascar. – 1. Holotype, SMNS ZI 30424 (L: 52.7 mm); – 2. holotype, apertual view; – 3. paratype 1, CK nº 2557 (L: 55.1 mm); – 4. paratype 2, SMNS ZI 30425 (L: 48.6 mm); – 5. paratype 3, CK nº 2532 (L: 45.3 mm); – 6. paratype 4, SMNS ZI 30426 (L: 44 mm); – 7. paratype 5, SMNS ZI 30427 (L: 45.4 mm); – 8. paratype 6, ex coll. CK nº 2532 ded. to NMC (L: 43.7 mm), north of Taolañaro (Fort Dauphin); – 9. paratype 7, CK nº 2531, (L: 32.5 mm). – Photographs: A. SCHULTHEISS (SMNS).

Plate 2

Figs. 1–9. *Conus pennaceus vezoi* n.ssp. from Maromitiliky, Madagascar. – 1. Holotype, SMNS ZI 30438 (L: 50.1 mm); – 2. holotype, apertual view; – 3. paratype 1, CB (L: 50.7 mm); – 4. paratype 2, CB (L: 54.1 mm); – 5. paratype 3, CB (L: 52.9 mm); – 6. paratype 4, CB (L: 44.1 mm); – 7. paratype 5, CB (L: 42.9 mm); – 8. paratype 6, CB (L: 43.2 mm); – 9. paratype 7, CB (L: 42.9 mm). – Photographs: A. SCHULTHEISS, (SMNS).

Plate 3

Figs. 1–2. *Conus pennaceus pennaceus* Born, 1778 from Conducia Bay, N Mozambique. – 1. Coll. DA MOTTA SMNS ZI 30449 (L: 47.7 mm); – 2. coll. DA MOTTA SMNS ZI 30450 (L: 47.6 mm). – Fig. 3. *Conus pennaceus* ("*elisae* form") from Conducia Bay, N Mozambique, coll. DA MOTTA SMNS ZI 30451 (L: 48.0 mm). – Figs. 4–7. *Conus pennaceus pennaceus* Born, 1778. – 4. From Mossuril, N Mozambique, coll. DA MOTTA SMNS ZI 30452 (L: 60.6 mm); – 5. from Memba Bay, N Mozambique, coll. RÖCKEL SMNS ZI 30453 (L: 68.8 mm); – 6. from Nacala, N Mozambique, coll. RÖCKEL SMNS ZI 30454 (L: 56.7 mm); – 7. from Nacala, N Mozambique, coll. DA MOTTA SMNS ZI 30455 (L: 46.5 mm). – Figs. 8–9. *Conus pennaceus* Born, 1778. – 8. From Ilha do Bazaruto, S Mozambique, coll. RÖCKEL SMNS ZI 30456 (L: 48.2 mm); – 9. from Massinga, S Mozambique, coll. RÖCKEL SMNS ZI 30457 (L: 57.2 mm). – Photographs: A. SCHULTHEISS (SMNS).

Plate 4

Figs. 1–2. *Conus echo* Lauer, 1988 from Somalia. – 1. Coll. RÖCKEL SMNS ZI 30458 (L: 52.2 mm); – 2. coll. RÖCKEL SMNS ZI 30459 (L: 52.0 mm). – Fig. 3. *Conus lohri* Kilburn, 1972 from Port Edward, Natal, coll. RÖCKEL SMNS ZI 30460 (L: 60.0 mm). – Figs. 4–5. *Conus pennaceus* Born, 1778 from Nosy Be (an error, in Madagascar north of Morombe). – 4. Coll. DA MOTTA SMNS ZI 9104 (L: 62.0 mm); – 5. coll. DA MOTTA SMNS ZI 9103 (L: 48.0 mm). – Figs. 6–7. *Conus pennaceus* Born, 1778 from Morombe, Madagascar. – 6. SMNS ZI 30461 (L: 48.7 mm); – 7. SMNS ZI 30462 (L: 43.2 mm). – Figs. 8–9. *Conus pennaceus* Born, 1778 from Ambatomilo, Madagascar. – 8. SMNS ZI 9109/2 (L: 54.8 mm); – 9. SMNS ZI 9109/1 (L: 53.3 mm). – Photographs: A. SCHULTHEISS (SMNS).

Plate 5

Figs. 1–9. *Conus pennaceus* Born, 1778 from Ambatomilo, Madagascar. – 1. SMNS ZI 9108/2 (L: 51.2 mm); – 2. SMNS ZI 9112 (L: 55.3 mm); – 3. SMNS ZI 9113 (L: 51.5 mm); – 4. SMNS ZI 9116 (L: 54.3 mm); – 5. SMNS ZI 9111 (L: 57.6 mm); – 6. SMNS ZI 9117 (L: 55.7 mm); – 7. SMNS ZI 9115 (L: 52.9 mm); – 8. SMNS ZI 9109/3 (L: 54.0 mm); – 9. SMNS ZI 9108/1 (L: 57.9 mm). – Photographs: A. SCHULTHEISS (SMNS).

Plate 6

Fig. 1. *Conus pennaceus* Born, 1778 from Ambatomilo or Beheloka?, Madagascar, CK nº 859 (L: 60.3 mm). – Fig. 2. *Conus pennaceus corbieri* Blöcher, 1994, Holotype, from Salary, Madagascar, SMNS ZI 9110 (L: 53.9 mm). – Fig. 3. *Conus pennaceus* Born, 1778 found between Manombo and Morombe, Madagascar, SMNS ZI 30463 (L: 35.0 mm). – Figs. 4–8. *Conus pennaceus behelokensis* Lauer, 1989 from Beheloka, Madagascar. – 4. Coll. DA MOTTA SMNS ZI 9106/1 (L: 56.4 mm); – 5. coll. RÖCKEL SMNS ZI 30464 (L: 58.2 mm); – 6. coll. DA MOTTA SMNS ZI 9107 (L: 61.5 mm); – 7. CK nº 1067 (L: 42.6 mm); – 8. coll. DA MOTTA SMNS ZI 9106/2 (L: 44.0 mm). – Fig. 9. *Conus textile* Linné, 1758 ("*sirventi* form") from south of Toliara, between Anakao and Beheloka, Madagascar, SMNS ZI 30465 (L: 54.3 mm). – Photographs: A. SCHULTHEISS (SMNS).

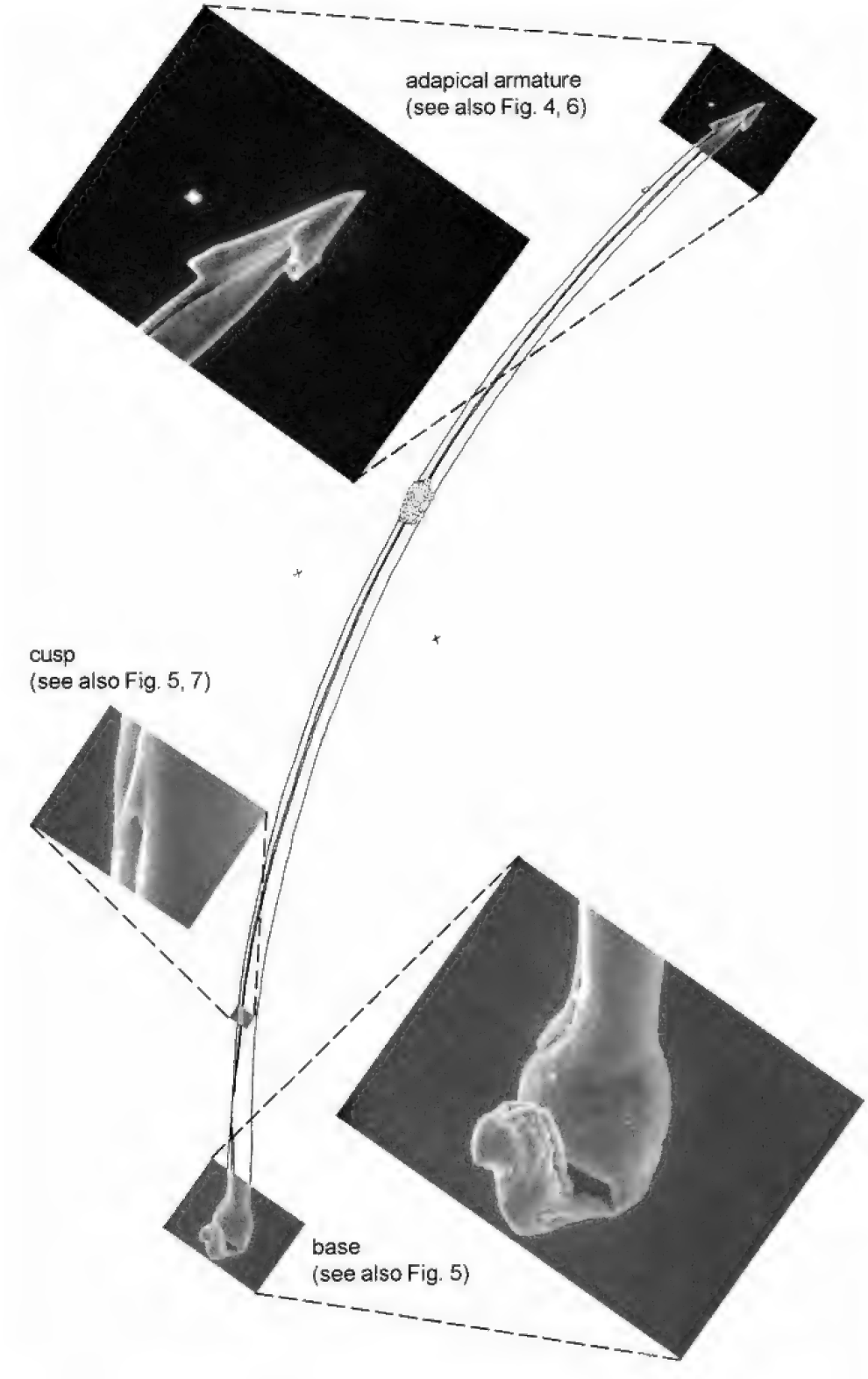
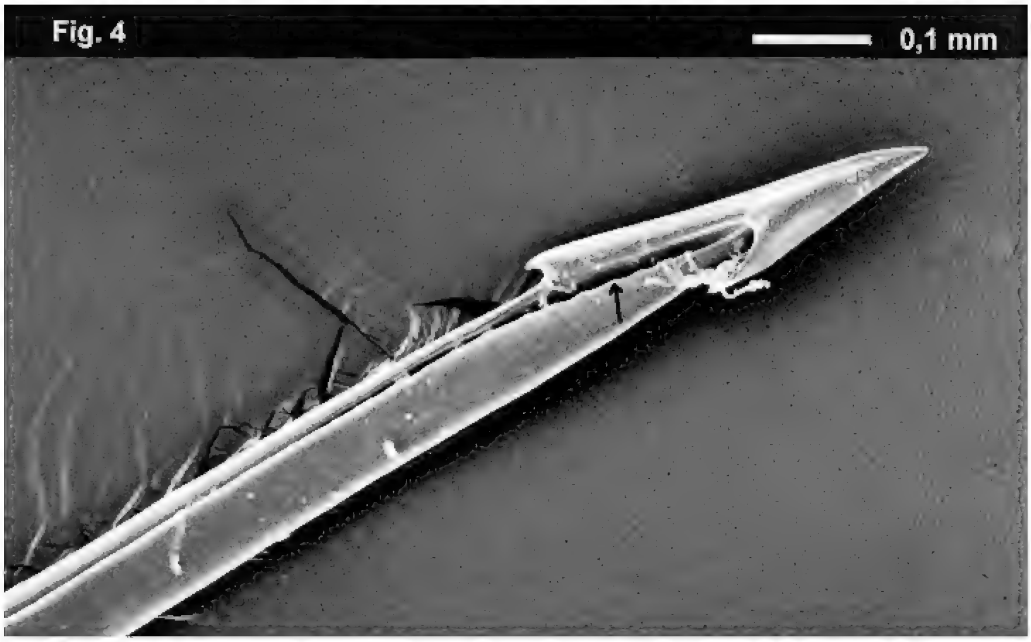
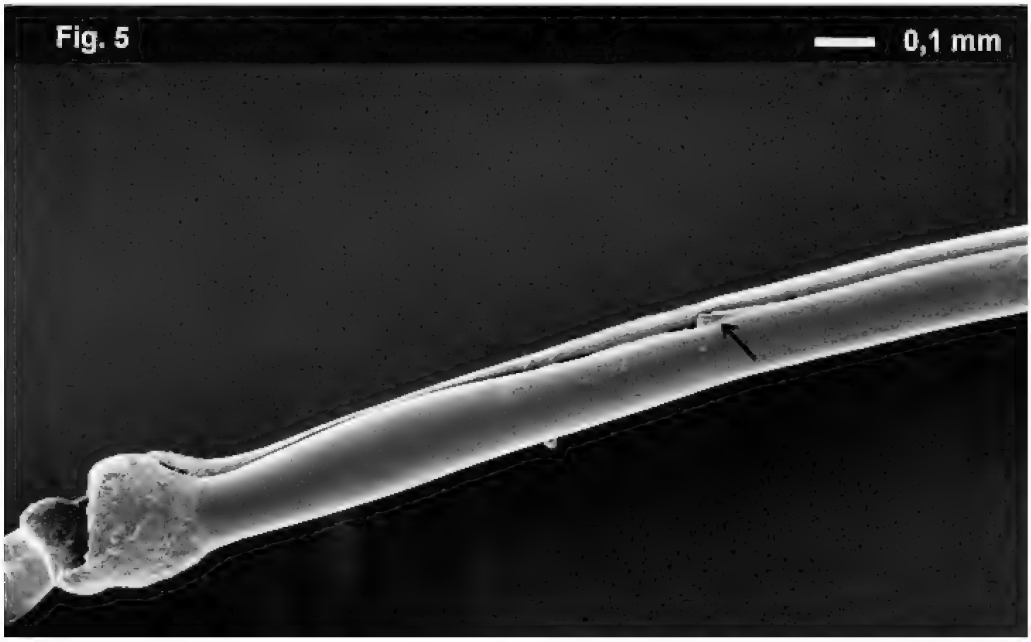


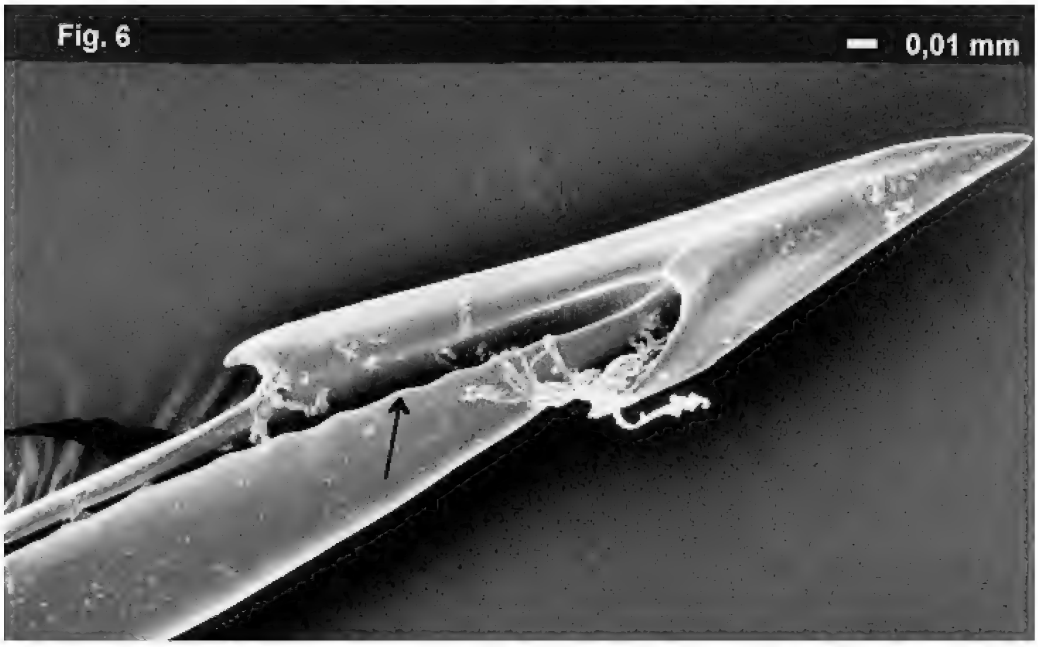
Fig. 3. Radular teeth from *Conus pennaceus vezoi* n.ssp. (holotype). – Photographs: E. MATERNA-MORRIS, Karlsruhe.

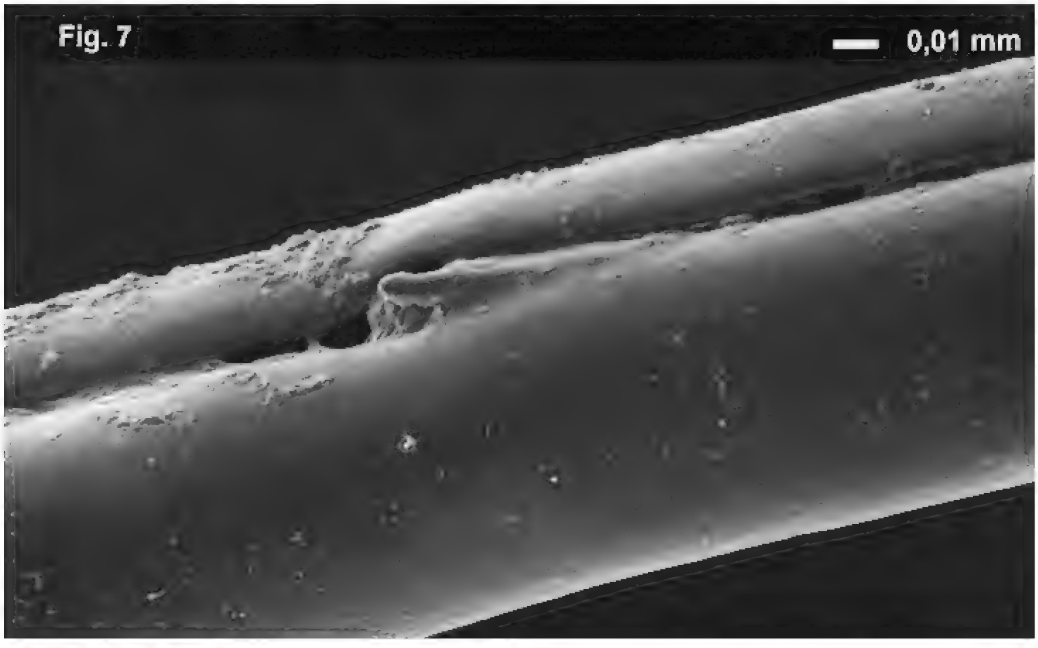




Figs. 4–5. Radular teeth from *Conus pennaceus vezoi* n.ssp. (holotype). – 4. Adapical armature with undulated internal fold *(arrow)*; – 5. base and part of the shaft with cusp *(arrow)* at the inner fold. – Photographs: S. LEIDENROTH (SMNS).

Description [terminology after RÖCKEL et alii (1995: 20, 21]): Generally medium-sized, moderately solid. Last whorl ventricosely conical to ovate; outline convex, less so basally; left side may be sigmoid. Aperture wider at base. Shoulder angulate to rounded. Spire usually of moderate height; outline straight, rarely convex. Teleoconch sutural ramps flat to sigmoid; middle ramps with 3–4 weak spiral





Figs. 6–7. Radular teeth from *Conus pennaceus vezoi* n.ssp. (holotype). – 6. Detail of the adapical armature with undulated internal fold *(arrow);* – 7. detail of the cusp at the inner fold. – Photographs: S. LEIDENROTH (SMNS).

grooves, late ramps with numerous spiral striae. Weak spiral ribs at base of last whorl.

Ground colour bluish white to blue. Last whorl overlaid with light to dark brown forming axial and/or 3 spiral bands. Fine dark brown lines edging tiny to large ground-colour tents that may fuse axially. Brown overlying flecks, blotches and bands with close-set very fine axial dashes and variably set fine spiral rows of dark-

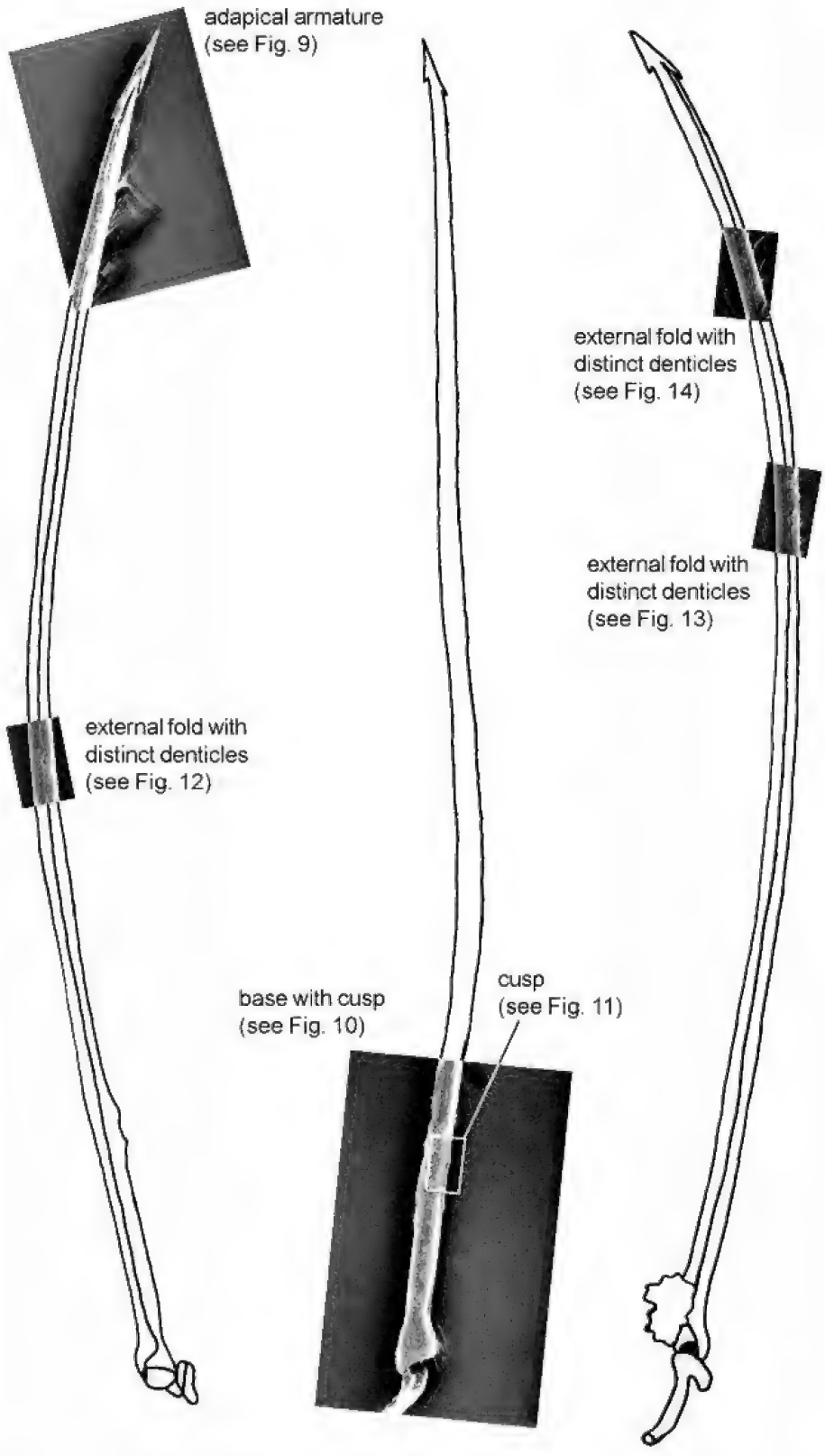
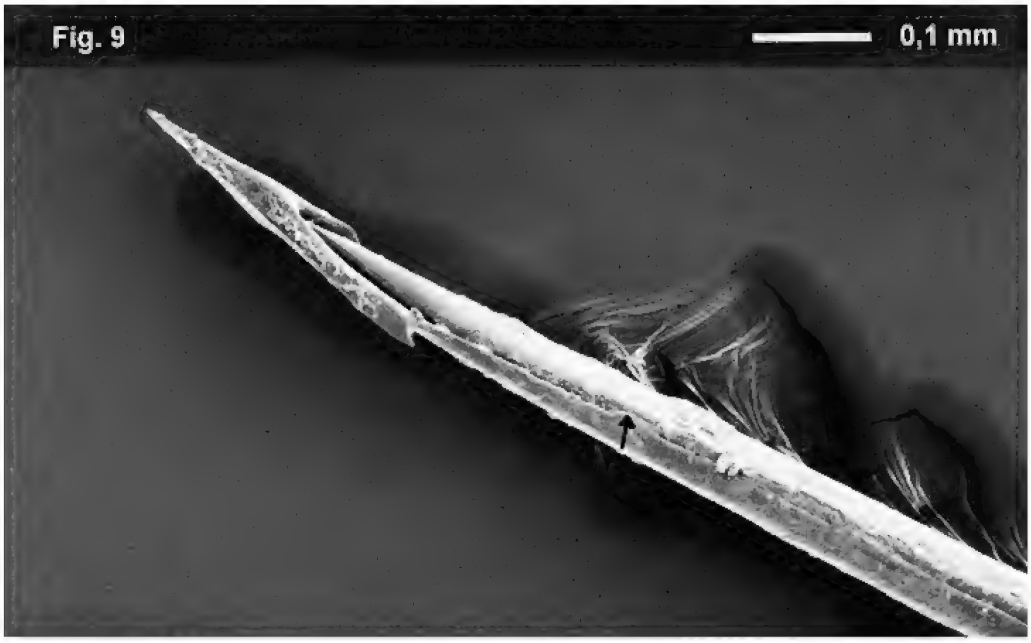
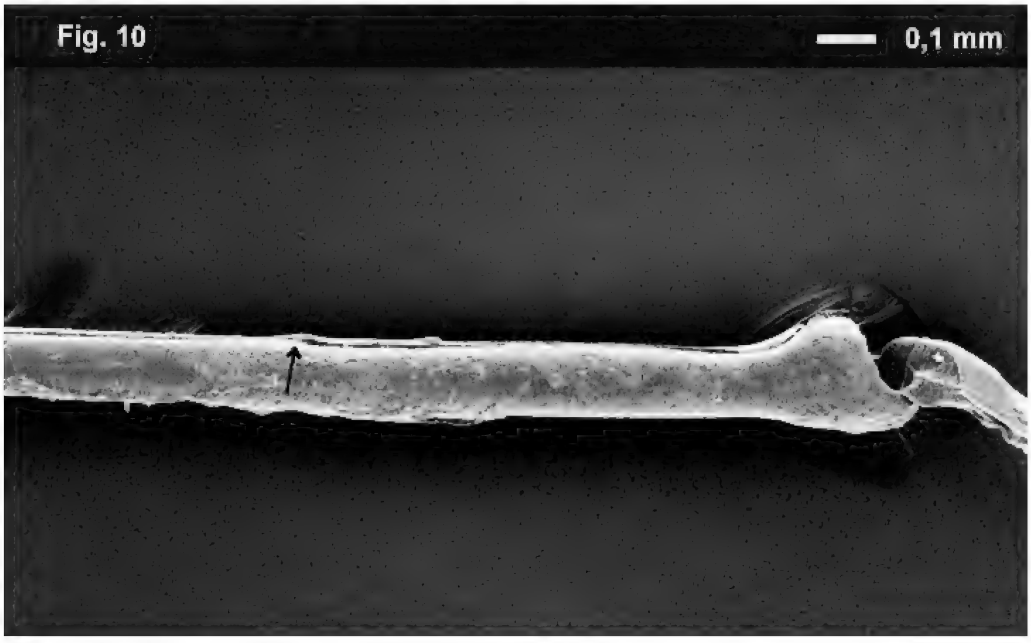


Fig. 8. Radular teeth from *Conus textile* ("form *sirventi*"), Madagascar. – Photographs: S. LEIDENROTH (SMNS).

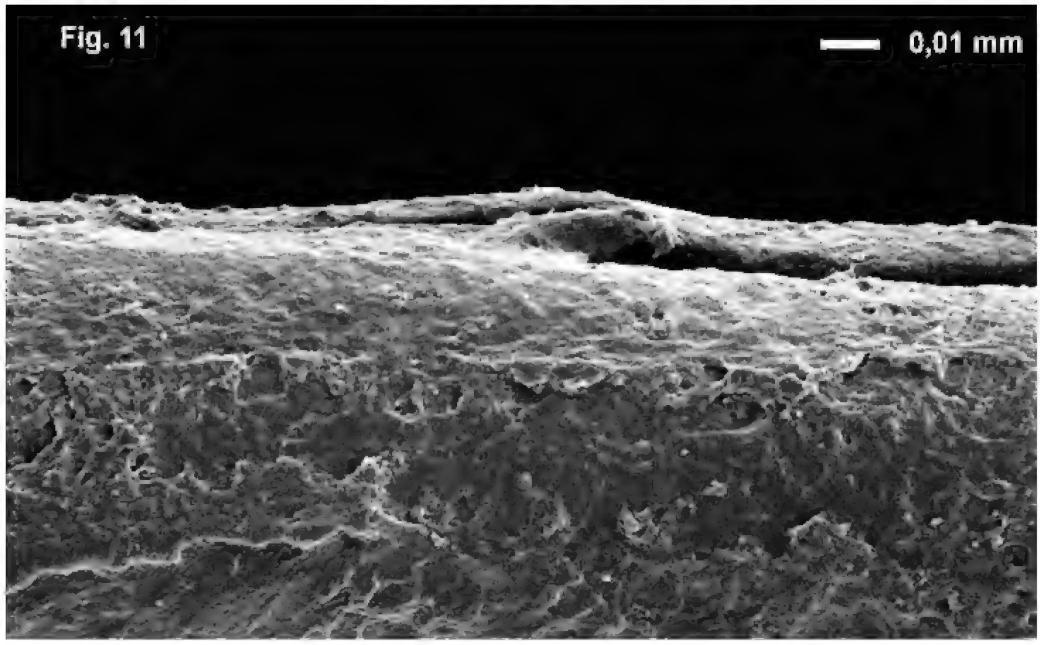


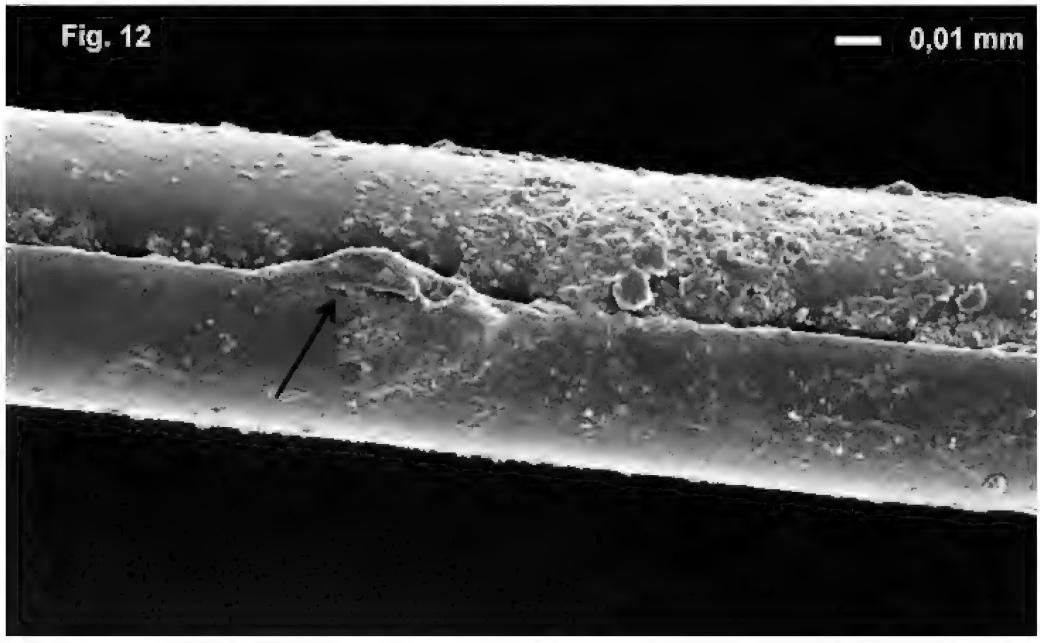


Figs. 9–10. Radular teeth from *Conus textile* ("form *sirventi*"), Madagascar. – 9. Adapical armature. At the shaft the external fold shows a distinct denticle *(arrow);* – 10. base and part of the shaft with cusp *(arrow)* at the inner fold. – Photographs: S. LEIDENROTH (SMNS).

er brown dots interspersed with tiny ground-colour markings. Basal part of columella white to bluish white. Apex red to purple. Following ramps matching last whorl in colour pattern. Aperture bluish white.

Habitat: At Taolañaro the coast has rock benches alternating with areas of white sand. The rocky areas may form platforms extending into the sea and giving rise to

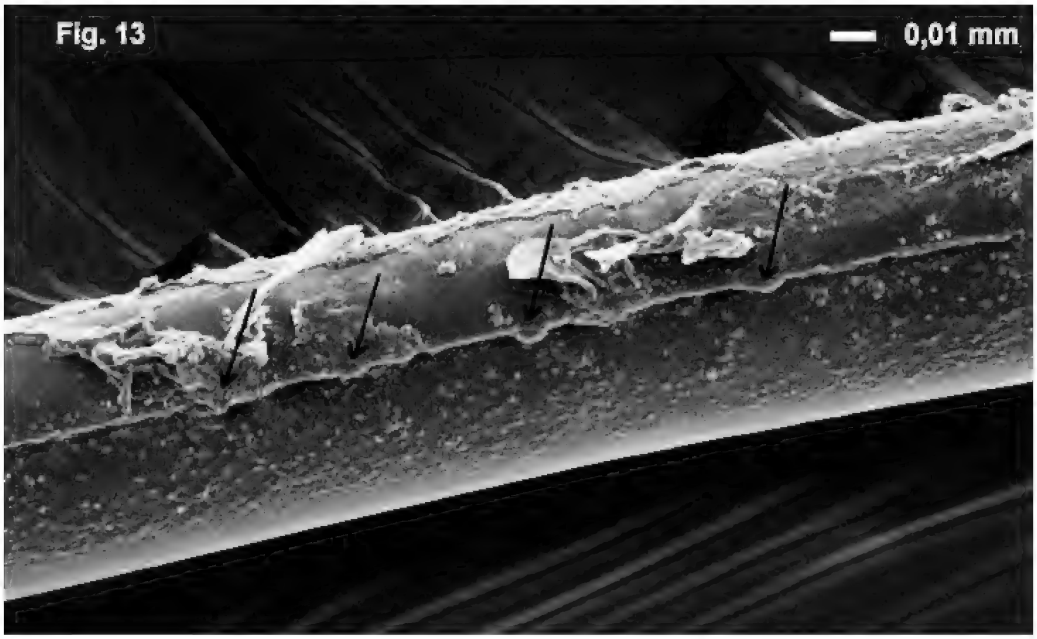


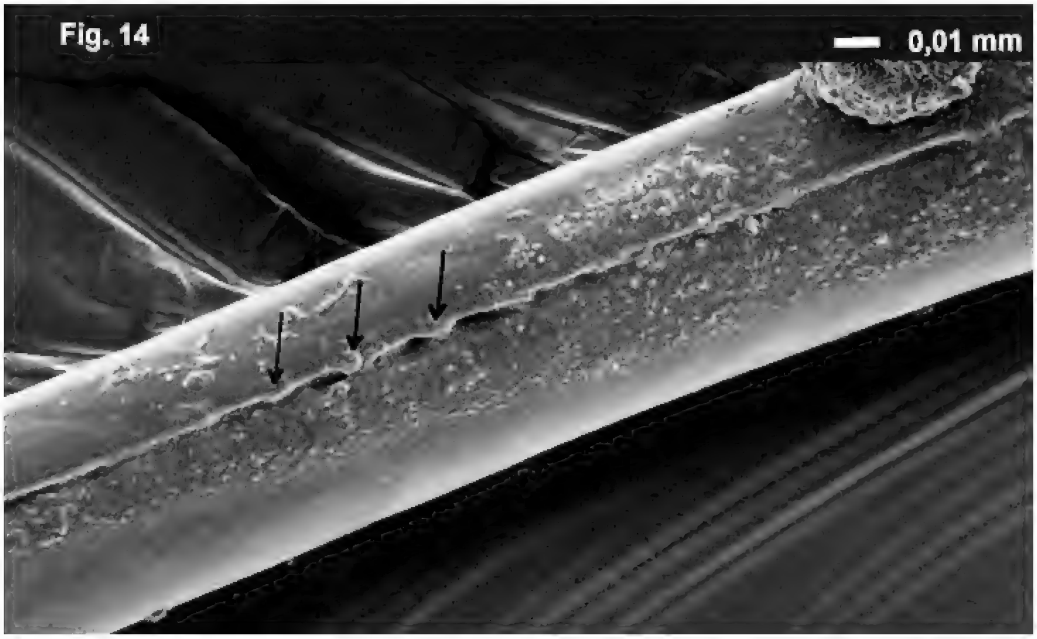


Figs. 11–12. Radular teeth from *Conus textile* ("form *sirventi*"), Madagascar. – 11. Detail of the cusp at internal fold; – 12. part of the shaft with a big denticle *(arrow)* at the external fold. – Photographs: S. LEIDENROTH (SMNS).

sheltered tide-pools, where coral may live protected from ponding waves. *C. p. tsara* occurs within these pools as well as at the seaward base of the rocky platforms.

Range: Known only from the area around Taolañaro, SE Madagascar.





Figs. 13–14. Radular teeth from *Conus textile* ("form *sirventi*"), Madagascar; different parts of the shaft with denticles *(arrows)* at the external fold. – Photographs: S. Leidenroth (SMNS).

4.2. *Conus pennaceus vezoi* n.ssp. (Plate 2)

Holotype (with periostracum, parts of the animal and radula): SMNS ZI 30438 (L: 50.1 mm, MD: 26.7 mm).

Paratype 1: CB (L: 50.7 mm, MD: 25.8 mm). – Paratype 2: CB (L: 54.1 mm, MD: 30.1 mm). – Paratype 3: CB (L: 52.9 mm, MD: 29.9 mm). – Paratype 4: CB (L: 44.1 mm, MD: 22.1 mm). – Paratype 5: CB (42.9 mm, MD: 21.2 mm). – Paratype 6: CB (L: 43.2 mm,

MD: 22.7 mm). – Paratype 7: CB (L: 42.9 mm, MD: 24.0 mm). – Paratype 8 (with periostracum and parts of the animal): SMNS ZIa 30439 (L: 52.1 mm, MD: 27.2 mm). – Paratype 9 (with periostracum and parts of the animal): SMNS ZIa 30440 (L: 46.3 mm; MD: 24.4 mm). – Paratype 10 (with periostracum and parts of the animal): SMNS ZIa 30441 (L: 33 mm, MD:16.3 mm). – Paratype 11: CB (L: 50,0 mm, MD: 25.3 mm). – Paratype 12: CB (L: 46.8 mm, MD: 25.5 mm). – Paratype 13: CB (L: 45.5 mm, MD: 24.0 mm). – Paratype 14: CB (L: 44.6 mm, MD: 23.2 mm). – Paratype 15: CB (L: 44.4 mm, MD: 24.0 mm). – Paratype 16: CB (L: 41.5 mm, MD: 21.1 mm). – Paratype 17: CB (L: 41.3 mm, MD: 20.3 mm). – Paratype 18: CB (L: 39.2 mm, MD: 20.0 mm). – Paratype 19: CB (L: 36.4 mm, MD: 18.7 mm). – Paratype 20: ex CK nº 2487 ded. to NMC (L: 53.5 mm, MD: 30.0 mm). – Paratype 21–27: SMNS ZI 30442–30448 (L: 48.3–26.1 mm, MD: 24.0–13.7 mm).

Type Locality: SW Madagascar, Maromitiliky, 25 km (by air-line) south of Pointe Beheloka south of Toliara (Fig. 2).

Etymology: This local race is named after the ethnic group of the Vezo that lives in SW Madagascar. The Vezo almost exclusively subsist on marine animals and give support to marine shell research since many years. Therefore they should be honoured with this naming.

Description [see Röckel et alii (1995)]: Generally medium-sized, moderately solid to solid; relative weight may vary by 20% between the lighter conoid-cylindrical form and the more solid conical form. Shells with conoid-cylindrical last whorl intergrade into shells with conical to ventricosely conical last whorl; left side slightly convex to convex, right side straight to slightly convex, more convex at shoulder. Aperture wider at base. Shoulder angulate to subangulate, sometimes rounded. Spire of low to moderate height; outline concave to convex, apex rarely domed. Teleoconch sutural ramps flat; middle ramps with 3–4 faint spiral grooves, late ramps with very faint spiral striae. Last whorl with weak spiral ribs at base.

Ground colour white to whitish blue or violet. Last whorl usually overlaid with brown to blackish brown sometimes leaving scattered ground-colour tents or clusters of tents; seldom with extensive tentmark pattern. Brown areas may be encircled with rows of brown dots and dashes interspersed by tiny to small ground-colour markings; rows may be absent. Basal part of columella white. Apex red to faint purple. Following teleoconch sutural ramps matching last whorl in colour pattern. Aperture white suffused with blue or violet.

Periostracum olive, variable in thickness, still translucent.

Radular teeth from *C. pennaceus* are figured or described by Kohn (1959), Hawaii; Kilburn (1972), South Africa; James (1980), Hawaii; Bandel (1984), Port Sudan; Nybakken (1990), Hawaii. The comprehensive description in Röckel et alii (1995) says "Radular teeth with a laterally adapical barb opposite a larger second barb; serration external, extending $^1/_3$ of the length down the shaft; a distinct cusp located about $^1/_3$ of the length from the base; waist and basal spur absent." The animals feed on molluscs. In general, shell/tooth ratio is about 7.7 (James 1980). This value does not at all agree with those published by Nishi & Kohn (1999).

Only from the holotype of *C. pennaceus vezoi* n.ssp. we had the possibility to examine the radular teeth (Figs. 3–7). For the first time, radular teeth of a *C. pennaceus* specimen from Madagascar are presented. For the specimen of *C. pennaceus vezoi* n.ssp. the tooth length of the examined teeth is T_{L1} = 6.45 mm, T_{L2} = 5.90 mm, T_{L3} = 6.40 mm, T_{L4} = 6.25 mm. All examined teeth show a distinct cusp $^1/_7$ of the length from the base. Between cusp and barbs is a fine undulation at the anterior part of the inner fold of the shaft (serration according Nishi & Kohn, 1999: 487). Relative tooth length (T_L/S_L), relative first barb length ($B1_L/T_L$) and relative second barb

length ($B2_L/T_L$) were taken as defined by NISHI & KOHN (1999: 484). Table 1 shows that there is no overlap between our values and those given by NISHI & KOHN (1999: 490). There are striking differences between the populations from the Western Indian Ocean, *C. p. vezoi* n.ssp. from Madagascar and *C. pennaceus* from the Maldives.

Habitat: At the type locality a poorly developed coral reef separates a small and relatively shallow lagoon from the open sea. *C. p. vezoi* n.ssp. occurs subtidally inside the lagoon as well as near the reef edge outside the lagoon. The surface condition of the living shells suggest exposure to fishes that feed on *Conus* and to epibionts.

Range: Known only from the type locality in SW Madagascar.

C. pennaceus tsara n. ssp. (Taolañaro) L: 30–55 mm RW: 0.09–0.24 g/mm RD: 0.54–0.65 PMD: 0.70–0.81 RSH: 0.11–0.15
C. pennaceus vezoi n. ssp. (Maromitiliky) L: 27–54 mm RW: 0.09–0.41 g/mm (conical form) –0.33 g/mm (conoid-cylindrical form) RD: 0.50–0.63 PMD: 0.76–0.87 RSH: 0.07–0.15
C. pennaceus behelokensis Lauer, 1989 (Beheloka) L: 40–62 mm RW: 0.20–0.38 g/mm RD: 0.56–0.62 PMD: 0.75–0.84 RSH: 0.08–0.15
C. pennaceus population [about 100 km (by air-line) north of Toliara (Ambatomilo area)] L: 50–58 mm RW: 0.26–0.44 g/mm (may vary by 20%) RD: 0.59–0.64 PMD: 0.70–0.81 RSH: 0.10–0.15
C. p. pennaceus Born, 1778 (from northern Mozambique) L: 48–70 mm RW: 0.32–0.46 g/mm (variation for L = 57 mm) RD: 0.50–0.64 PMD: 0.78–0.86 RSH: 0.08–0.15

4.3. Shell morphometry

The shell morphometry is given for the first time for ssp. *tsara,* ssp. *vezoi,* and the shells from Ambatomilo. For ssp. *behelokensis* and ssp. *pennaceus* the shell morphometry given by RÖCKEL et alii (1995) was revised.

The box (see p. 22) with the quantitative informations shows a high uniformity in the relative spire height (RSH) between all populations measured. The main differences occur in relative weight (RW), general shape of the last whorl (RD, PMD) and in shell size (L).

4.4. Discussion

In the nominal subspecies of *C. pennaceus* the apex of the shell is usually domed or convex, rarely straight. In all morphs of *C. pennaceus* from Madagascar, the apex is generally straight, sometimes convex and rarely domed (about 5% of the material examined had a domed apex). In addition, the shells of *C. p. pennaceus* grow larger than shells of *C. pennaceus* from Madagascar (70 mm versus 62 mm).

C. p. tsara n.ssp. additionally differs from the nominal subspecies by the uniformity of its colour pattern and its less solid shell that is usually less conical or even ovate.

C. p. vezoi n.ssp. additionally differs from the nominal subspecies in its uniform colour pattern that does not occur in N Mozambique.

In Madagascar, *C. p. tsara* is the subspecies with the lightest shell: *C. p. vezoi, C. p. corbieri* Blöcher, 1994 and the shells from the Ambatomilo area are distinctly

Tab. 1. Radular tooth characters of *Conus pennaceus.*

	T_L/S_L	$B1_L/T_L$	$B2_L/T_L$
C. pennaceus vezoi (holotype)	0.126	0.029	0.046
C. pennaceus (total) After NISHI & KOHN (1999: 490)	0.051–0.081	0.038–0.076	0.057–0.118
C. pennaceus (Maledives) After NISHI & KOHN (1999: 490)	0.064–0.070	0.039–0.044	0.070–0.084
C. pennaceus (Hawaii) After NISHI & KOHN (1999: 490)	0.051–0.081	0.043–0.076	0.081–0.118

Tab. 2. Radular tooth characters of *Conus textile.*

	T_L/S_L	$B1_L/T_L$	$B2_L/T_L$
C. textile ("form *sirventi*") (Madagascar)	0.116	0.035	0.048
C. textile (total) After NISHI & KOHN (1999: 490)	0.103–0.149	0.021–0.035	0.040–0.063

heavier. As for *C. p. behelokensis* Lauer, 1989, the lightest shell of this subspecies match the heaviest shells of *C. p. tsara* in weight. Shells of *C. p. behelokensis, C. p. corbieri* and shells from Ambatomilo grow larger than shells of *C. p. tsara.* In addition, *C. p. tsara* differs in its pattern from all variants elsewhere in Madagascar.

C. p. vezoi is separated from its Madagascan congeners by the shell dimorphism within the population: light and conoid-cylindrical shells occur together with heavier and more conical shells. In addition, *C. p. vezoi* is separated from *C. p. tsara* by relative weight, shape and colour pattern of the shells. *C. p. behelokensis* has larger shells than *C. p. vezoi* that are distinctly lighter in weight and never have a conoid-cylindrical shape. The only difference in colour pattern is the usually lighter brown tone in *C. p. behelokensis. C. p. corbieri* differs from *C. p. vezoi* in its larger and ventricosely conical rather than conoid-cylindrical shells that have a completely different colour pattern. The *C. pennaceus* shells from Ambatomilo never have a conical or conoid-cylindrical shape as seen in *C. p. vezoi* and their colour patterns do not include the *vezoi*-pattern. In addition they grow larger.

5. Radular teeth – a comparison between *Conus pennaceus vezoi* n.ssp. (Figs. 3–7) and *Conus textile* Linné, 1758 ("form *sirventi*") (Figs. 8–14)

Fortunately we also had the possibility to examine radular teeth of a *C. textile* Linné, 1758 ("form *sirventi*") specimen from Madagascar. Both, *C. textile* and *C. pennaceus* are molluscivorous and should therefore have similar radular teeth.

Radular teeth from *C. textile* are figured or described by Bergh (1895), Philippinen; Peile (1939), Andaman Isl.; Kohn (1959), Hawaii; James (1980), Hawaii; Bandel (1984), Port Sudan; Rolan (1993), no locality given. The standard description in Röckel et alii (1995) says "Radular teeth comparatively long ... and slender, with 2 opposed barbs adapically; long but weak to obsolete serration ending in a weak cusp about $^1/_7$ of the length from the base; basal spur absent ...". James (1980) reported an extreme shell/tooth ratio of 3.5 while Kohn (1963) stated ratios of 8.0 and 9.0.

For the first time radular teeth of *C. textile* from Madagascar are shown (Plate 6/Fig. 9). The tooth length of the examined teeth is T_{L1} = 6.45 mm, T_{L2} = 6.30 mm, T_{L3} = 6.50 mm. All examined teeth have a distinct cusp at $^1/_7$ of the total length from the base. A regular continuous serration (Nishi & Kohn, 1999: 487) could not be observed due to the poor condition of the teeth. However the margin of the external fold is undulated partially forming distinct denticles. T_L/S_L, $B1_L/T_L$ and $B2_L/T_L$ are measured as defined by Nishi & Kohn (1999). Table 2 shows a striking agreement between our values and those given by Nishi & Kohn (1999).

In Madagascar the radular teeth of *C. textile* Linné, 1758 ("form *sirventi*") and *C. pennaceus vezoi* differ in tooth/shell ratio = T_L/S_L (0.116 versus 0.126) and the undulation of the external fold in *C. textile* (Tab. 1). As for the relative length of the barbs, *C. p. vezoi* n.ssp. and *C. textile* from Madagascar ("form *sirventi*") reveal hardly any difference.

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